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# Diet Dynamics of the Adult Piscivorous Fish Community in Spirit Lake, Iowa, USA 1995–1997

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**Keywords**

freshwater fish, adult, diet, piscivory, diet similarity, temporal dynamics, asynchronous changes, animal ecology

**Disciplines**

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Abstract – Diets of adults of six important piscivorous fish species, black crappie *Pomoxis nigromaculatus*, largemouth bass *Micropterus salmoides*, northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieui*, walleye *Stizostedion vitreum*, and yellow perch *Perca flavescens* were quantified in Spirit Lake, Iowa, USA from May to October in 1995–1997. Forty-one prey taxa were found in the diets of these species, including 19 species of fish. The most important prey taxa overall were yellow perch, amphipods and dipterans. Diets of northern pike and walleye were dominated by yellow perch. Largemouth bass diets included large percentages of both yellow perch and black bullhead *Ameiurus melas*. Smallmouth bass diets included large percentages of both yellow perch and crayfish. Black crappie and yellow perch diets were dominated by invertebrates, primarily amphipods and dipterans. There were pronounced differences in diets among species, among size classes within species and over time. Most of the dominant prey taxa we documented in the diets of piscivorous species were in accordance with previous studies, but a few deviated significantly from expectations. Many of the temporal diet changes were asynchronous among piscivorous species and size classes, suggesting different responses to common prey resources over time.

Key words: freshwater fish; adult; diet; piscivory; diet similarity; temporal dynamics; asynchronous changes

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**Un resumen en español se incluye detrás del texto principal de este artículo.**

## Introduction

Fisheries biologists have long appreciated the importance of feeding and food habits to the ecology and production dynamics of fish stocks (Gerking 1994). Likewise, there is recognition that the feeding activities of fish often have significant impacts on their prey (Northcote 1988). More recently, the strong effects of predatory fish have been shown to not only deplete their immediate prey supply, but modify the aquatic food web (Carpenter & Kitchell 1993). A key element in understanding the relationship between aquatic predators and prey is quantifying the rate of energy transfer through consumption. The first step in this process is a detailed analysis of the diet dynamics of the predator species.

Largemouth bass *Micropterus salmoides* (Lacepède), northern pike *Esox lucius* (Linnaeus), smallmouth bass *Micropterus dolomieui* (Lacepède), and walleye *Stizostedion vitreum* (Mitchell) are well-documented piscivorous species in many aquatic ecosystems (Mann 1982; Knight et al. 1984; Hartman & Margraf 1992; Hodgson et al. 1997). Piscivory by black crappie *Pomoxis nigromaculatus* (Lesueur) and yellow perch *Perca flavescens* (Mitchell), although known to occur, appears to be less prominent and these two species are more flexible in response to availability of suitable fish prey and relative size of predators and prey (Ellison 1984; Knight et al. 1984; Paszkowski & Tonn 1994; Hodgson et al. 1997). Although some studies have considered diets of two or three of the above species and their effects on interspecific interactions (Vigg et al. 1991; Hodgson et al. 1997), few studies have examined complex piscivorous communities comprised of more than two or three species. We are not aware of any that examined these six species simultaneously in a common system.

Spirit Lake, Iowa, USA provided an opportunity to study a diverse adult piscivorous community. The presence of six well-known species in a common environment allowed us to quantify their diets and explore diet similarities in response to a common suite of food resources. In addition, because diets of juveniles of these species (except northern pike) have been studied in Spirit Lake (Pelham et al. 2001), we were also able to compare adult diets with juvenile diets of the same species. The specific objectives of this study were to (1) characterize the diets of important members of the piscivorous community, (2) explore seasonal, annual, and size-related diet similarities within and among species, and (3) illustrate seasonal diet variation among species and between size classes within species in Spirit Lake.

## Study area

Spirit Lake (43°28′ N, 95°06′ W) is Iowa's largest natural lake, with a surface area of 2229 ha, a maximum depth of 7 m, and water quality classified as eutrophic (Bachman et al. 1995). Ice cover typically occurs from early December to early April, and summer water temperature peaks in July or August around 25°C with no thermal stratification. The littoral zone, which contains variable mixtures of primarily sand, cobble, and macrophytes, occupies roughly 14% of the lake's surface area. The offshore zone substrate is composed of primarily sand and silt. The littoral fish community, which includes all known species present (Pelham 2000), is described elsewhere (Pierce et al. 2001a, b). Because of the popular recreational fishery, the walleye population is augmented by annual fry stocking.

## Material and methods

### Data collection

Black crappie, largemouth bass, northern pike, smallmouth bass, walleye, and yellow perch were collected in Spirit Lake from early May to late October, 1995–1997. These six species are the dominant piscivorous species in the lake (Pierce et al. 2001b). About 70 percent of our fish were collected using an AC, boat-mounted electrofisher, and the rest were collected using a variety of gears including beach seine, fyke nets, gillnets, and angling. We conducted electrofishing and beach seining after sunset, angling during the daytime, and fyke netting and gillnetting both during daytime and at night. Each fish was measured to the nearest 2.5 mm in total length and weighed to the nearest 14 g. Only fish $\geq$150 mm in total length were examined for this study. Stomach contents were flushed out using a water pump (Baker & Fraser 1976), immediately bagged, labeled, put on ice in a cooler, and frozen within a few hours for later identification in the laboratory. All fish were released alive immediately after stomach flushing. Because of potential contamination from water pumped in from the lake, zooplankton was excluded from the analysis of stomach contents.

Prey fish were identified to species, and invertebrates were identified either to phylum, class, or order in the laboratory. Other vertebrate prey was identified to class. Wet weights of prey fish and crayfish were estimated using length–weight equations developed in this study. Prey length was measured to the nearest 1 mm and wet weight was measured to the nearest 0.1 g. We estimated total lengths of partially digested prey fish following Knight et al. (1984). Other invertebrates found in stomachs were counted and measured in length only. If more than 10 individuals of an invertebrate taxon were found in a stomach, a subsample of 10 randomly selected specimens were measured. Dry weights of other invertebrates were estimated using length–weight equations found in the literature (Smock 1980; Meyer 1989), and wet weight was assumed to be five times dry weight (Morin & Dumont 1994).

### Data analysis

Data were grouped according to piscivorous species, year, season, and size. Each of the three sampling years was divided into three seasons: spring (May and June), summer (July and August), and fall (September and October) to examine potential seasonal shifts in diets. We divided each piscivorous species into two size classes. Threshold lengths for assigning fish to small or large size classes were chosen to roughly equally divide the length range of each species in Spirit Lake. Threshold lengths were 203 mm for black crappie and yellow perch, 305 mm for largemouth bass, smallmouth bass and walleye, and 560 mm for northern pike (Liao et al. 2001). In total, six piscivorous species $\times$ 3 years $\times$ 3 seasons $\times$ 2 sizes led to 108 possible categories, hereafter referred to as comparison units.

We used the index of relative importance expressed as percentages (%IRI) to describe prey importance for comparison units. %IRI is a compound index and is composed of the percent frequency of occurrence (%O), percentage by weight (%W), and numerical percentage (%N) (Pinkas et al. 1971; Cortes 1997). Liao et al. (2001) compared several dietary importance indices and concluded that %IRI provides the optimal balancing of frequency of occurrence, numerical abundance, and abundance by weight of prey taxa in fish diets.

We calculated %W, %O, %N, IRI, and %IRI for each prey taxon in each comparison unit as follows:

$$\%W_i = \frac{100 \times W_i}{\sum_{i=1}^{n} W_i} \tag{1}$$

$$\%O_i = \frac{100 \times O_i}{\sum_{i=1}^{n} O_i} \tag{2}$$

$$\%N_i = \frac{100 \times N_i}{\sum_{i=1}^{n} N_i} \tag{3}$$

$$IRI_i = \%O_i \times (\%W_i + \%N_i) \tag{4}$$

$$\%IRI_i = \frac{100 \times IRI_i}{\sum_{i=1}^{n} IRI_i} \tag{5}$$

where $n$ is the total number of prey taxa found in a comparison unit. $W_i$ and $N_i$ are the total wet weight (g) and number of prey $i$ in a comparison unit, respectively. $O_i$ is the number of predator stomachs containing prey $i$ in a comparison unit. $IRI_i$ is the value of IRI for prey $i$ in a comparison unit.

Because diets of predators typically include several prey taxa, we used a multivariate approach to explore diet similarities among and within the six piscivorous species. The units of comparison in these analyses were the average diets of each combination of piscivorous species, size class, year and season; we used %IRI of each prey taxon in the diet of each comparison unit as input data. %IRI values were transformed as ($\log_{10}[x + 1]$) prior to analysis. First, we calculated pairwise similarities between comparison units using the Bray–Curtis similarity coefficient (Clarke & Warwick 1994). The resulting similarity matrix was then used as input for a nonmetric multidimensional scaling (MDS) ordination. Finally, we calculated Pearson correlations of MDS dimension scores with the transformed %IRI data for each prey taxon to assist interpretation of the ordination. Prey taxa with correlations explaining at least 50% of the variation with dimension scores and significant at the 5% level ($r \geq 0.7$, $P < 0.05$) were considered of major importance in defining dimensions and are shown on ordination axes. Similarity calculations and the MDS ordination were performed using PRIMER (Clarke & Warwick 1994; Carr 1997), and correlations were run using the CORR procedure of SAS (SAS Institute Inc. 1996). See Clarke & Warwick (1994) for a detailed discussion of this approach and procedures.

We tested for differences in diets among piscivorous species and size classes using a multivariate analysis of similarities (ANOSIM), which is roughly analogous to a univariate 2-way ANOVA, but uses a nonparametric, randomization approach (Clarke & Warwick 1994). ANOSIM uses a similarity matrix as input, in this case Bray–Curtis similarities among all comparison units, and is based on random permutations of similarities among and within main-effect groupings. The species main effect had six levels, and ANOSIM calculated pairwise tests among species in addition to the overall test of differences across all species. The ANOSIM was performed using PRIMER (Clarke & Warwick 1994; Carr 1997). See Clarke & Warwick (1994) for a detailed discussion of this approach to testing for differences in multivariate responses.

## Results

### Diet composition

The contents of 3101 stomachs from six species over 3 years revealed 41 recognizable prey taxa in the diets of the piscivorous community in Spirit Lake (Table 1). Values of %IRI in individual comparison units ranged from less than 0.1 to 100%. To focus attention on more important prey taxa, we arbitrarily designated major prey taxa as those with %IRI $\geq$ 20% in at least one comparison unit. Overall, 14 prey taxa were rated as major (Table 1). The three most important prey taxa were yellow perch, amphipods and dipterans, both in terms of percentage of comparison units with %IRI $\geq$ 20% and mean %IRI (Table 1). The three most important prey fish species were yellow perch, black bullhead *Ameiurus melas* (Rafinesque), and walleye (Table 1).

Table 1. Prey taxa found in the diets of the piscivorous community in Spirit Lake, Iowa, USA, 1995–1997.

| Taxon | Common name | Percent of comparison units with %IRI $\geq$ 20% | Mean %IRI |
|---|---|---|---|
| Fish | | | |
| *Ictiobus cyprinellus* | Bigmouth buffalo | 0 | <0.1 |
| *Ameiurus melas* | Black bullhead* | 9.6 | 7.8 |
| *Pomoxis nigromaculatus* | Black crappie | 0 | 0.6 |
| *Lepomis macrochirus* | Bluegill* | 1.9 | 1.6 |
| *Pimephales notatus* | Bluntnose minnow | 0 | <0.1 |
| *Cyprinus carpio* | Common carp | 0 | <0.1 |
| *Notropis atherinoides* | Emerald shiner | 0 | <0.1 |
| *Aplodinotus grunniens* | Freshwater drum* | 1 | 0.8 |
| *Notemigonus crysoleucas* | Golden shiner | 0 | <0.1 |
| *Lepomis cyanellus* | Green sunfish | 0 | <0.1 |
| *Etheostoma exile* | Iowa darter | 0 | 0.2 |
| *Etheostoma nigrum* | Johnny darter* | 1 | 0.6 |
| *Micropterus salmoides* | Largemouth bass | 0 | 0.5 |
| *Percina caprodes* | Northern logperch | 0 | 1.6 |
| *Micropterus dolomieui* | Smallmouth bass | 0 | 0.1 |
| *Notropis hudsonius* | Spottail shiner | 0 | 0.2 |
| *Stizostedion vitreum* | Walleye* | 5.8 | 4.7 |
| *Morone chrysops* | White bass | 0 | <0.1 |
| *Perca flavescens* | Yellow perch* | 51 | 36.5 |
| Invertebrates | | | |
| Amphipoda | Scuds* | 28.9 | 18.0 |
| Annelida | Worms | 0 | 0.2 |
| Coleoptera | Beetles | 0 | 0.1 |
| Decapoda | Crayfish* | 10.6 | 6.5 |
| Diptera | True flies* | 19.2 | 10.3 |
| Ephemeroptera | Mayflies* | 6.7 | 4.9 |
| Gastropoda | Snails* | 1.9 | 1.4 |
| Hemiptera | Water boatmen* | 1 | 1.0 |
| Hirudinea | Leeches | 0 | 0.1 |
| Hymenoptera | Wasps | 0 | < 0.1 |
| Lepidoptera | Moth | 0 | < 0.1 |
| Megaloptera | Hellgrammites | 0 | 0.1 |
| Nematoda | Roundworms | 0 | < 0.1 |
| Nematomorpha | Horsehair worms | 0 | < 0.1 |
| Neuroptera | Spongillaflies | 0 | < 0.1 |
| Odonata | Dragonflies/damselflies* | 2.9 | 1.5 |
| Orthoptera | Grasshopper | 0 | 0.2 |
| Plecoptera | Stoneflies | 0 | < 0.1 |
| Plecypoda | Clams/mussels | 0 | < 0.1 |
| Trichoptera | Caddisflies* | 1.9 | 1.1 |
| Other vertebrates | | | |
| Amphibia | Frog | 0 | < 0.1 |
| Aves | Duck | 0 | < 0.1 |

Major prey taxa, indicated by an asterisk (*) following the common names, were those with %IRI $\geq$ 20% in at least one comparison unit. Mean %IRI for a prey taxon was calculated as the average of individual comparison unit %IRI scores across all units.

To summarize general diet differences among the six piscivorous species over the study, we calculated average %IRI for the 14 major prey taxa (Table 2). There was a gradient among the six species in overall relative importance of fish and invertebrates in the diets ranging from northern pike, which ate fish exclusively, to yellow perch and black crappie whose diets were dominated by invertebrate prey. Walleye and largemouth bass diets had large percentages of fish, and smallmouth bass diets were split between similar percentages of invertebrates and fish (Table 2).

Northern pike diets were dominated by yellow perch, averaging nearly 72% in importance over the study (Table 2). Some differences between large and small northern pike diet were apparent. Small northern pike tended to concentrate on yellow perch (Fig. 1), whereas large northern pike included other fish species such as walleye, freshwater drum *Aplodinotus grunniens* (Rafinesque), and bluegill *Lepomis macrochirus* (Rafinesque) (Fig. 2) in addition to yellow perch. No invertebrate taxa were rated as major prey taxa in the diet of northern pike (Table 2).

Largemouth bass diets were dominated by yellow perch and black bullhead, averaging about 37 and 40% in importance over the study, respectively (Table 2). Yellow perch was the most important taxon overall in the diet of small largemouth bass, but other taxa such as black bullhead, walleye, black crappie, Iowa darter *Etheostoma exile* (Girard) and odonates were occasionally important (Fig. 1). Large largemouth bass diets were less diverse, mainly consisting of yellow perch and black bullhead (Fig. 2). Importance of yellow perch and black bullhead in the diet of large largemouth bass showed a gradual reversal from dominance of yellow perch in 1995 to dominance of black bullhead in 1997 (Fig. 2).

Walleye diets were dominated by yellow perch, which averaged nearly 60% in importance over the study (Table 2). With few exceptions, large walleye concentrated on yellow perch regardless of season (Fig. 2). While feeding primarily on yellow perch, small walleye included larger percentages of invertebrates such as dipterans, ephemeropterans, and trichopterans (Fig. 1). Importance of yellow perch tended to increase from spring to fall in small walleye diets, with invertebrate prey taxa such as dipterans and amphipods showing the opposite trend. There was a decline in the importance of yellow perch in the diet of small walleye from 1995 to 1997.

Smallmouth bass diets were dominated by yellow perch and crayfish, which averaged roughly 37 and 24% in importance over the study, respectively (Table 2). There was a tendency for crayfish to be more important in the diets of both small and large smallmouth bass in spring and summer, and yellow perch and other fish species to be more important in fall, although there were exceptions to this pattern (Figs 1 and 2). Small smallmouth bass diets included more small invertebrate taxa (Fig. 1) whereas large smallmouth bass ate more crayfish and walleye throughout the study (Fig. 2).

Table 2. Occurrence (%) and mean importance (%IRI) of major prey taxa in the diets of piscivorous species in Spirit Lake, Iowa, USA, 1995–1997.

| | Northern pike | | Largemouth bass | | Walleye | | Smallmouth bass | | Yellow perch | | Black crappie | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prey taxon | 0 (%) | Mean %IRI | 0 (%) | Mean %IRI | 0 (%) | Mean %IRI | 0 (%) | Mean %IRI | 0 (%) | Mean %IRI | 0 (%) | Mean %IRI |
| Fish | | | | | | | | | | | | |
| Black bullhead | – | – | 50 | 40.4 | 5.6 | 2.7 | – | – | – | – | – | – |
| Bluegill | 5.9 | 1.9 | – | – | – | – | – | – | 5.6 | 3.7 | 6.7 | 2.9 |
| Freshwater drum | 5.9 | 4.8 | – | – | – | – | – | – | – | – | – | – |
| Johnny darter | – | – | – | – | – | – | – | – | 5.6 | 2.3 | – | – |
| Walleye | 23.5 | 14.1 | – | – | 5.6 | 3.3 | 5.6 | 8 | – | – | – | – |
| Yellow perch | 94.1 | 71.8 | 44.4 | 37.1 | 83.3 | 59.9 | 55.6 | 37.3 | 5.6 | 3.8 | 6.7 | 5.7 |
| Invertebrates | | | | | | | | | | | | |
| Amphipoda | – | – | 5.6 | 3.2 | 11.1 | 6.2 | 5.6 | 3.0 | 83.3 | 49.9 | 73.3 | 49.8 |
| Decapoda | – | – | – | – | – | – | 44.4 | 23.9 | 16.7 | 10.9 | – | – |
| Diptera | – | – | 5.6 | 5.6 | 27.8 | 14.0 | 22.2 | 11.5 | 22.2 | 12.7 | 33.3 | 18.8 |
| Ephemeroptera | – | – | – | – | 5.6 | 5.8 | – | – | – | – | 26.7 | 17.1 |
| Gastropoda | – | – | – | – | – | – | – | – | 11.1 | 7.8 | – | – |
| Hemiptera | – | – | – | – | – | – | – | – | 5.6 | 2.1 | – | – |
| Odonata | – | – | 5.6 | 4.0 | – | – | – | – | 5.5 | 2.5 | 6.7 | 2.2 |
| Trichoptera | – | – | – | – | 5.6 | 2.2 | 5.6 | 3.3 | – | – | – | – |

Major prey taxa were defined as those with %IRI $\geq$ 20% in at least one comparison unit. Mean %IRI for a prey taxon was calculated as the average of all the unit %IRI values for that taxon. – indicates that a prey taxon was either not a major taxon or not found in the diet of a particular piscivorous species.

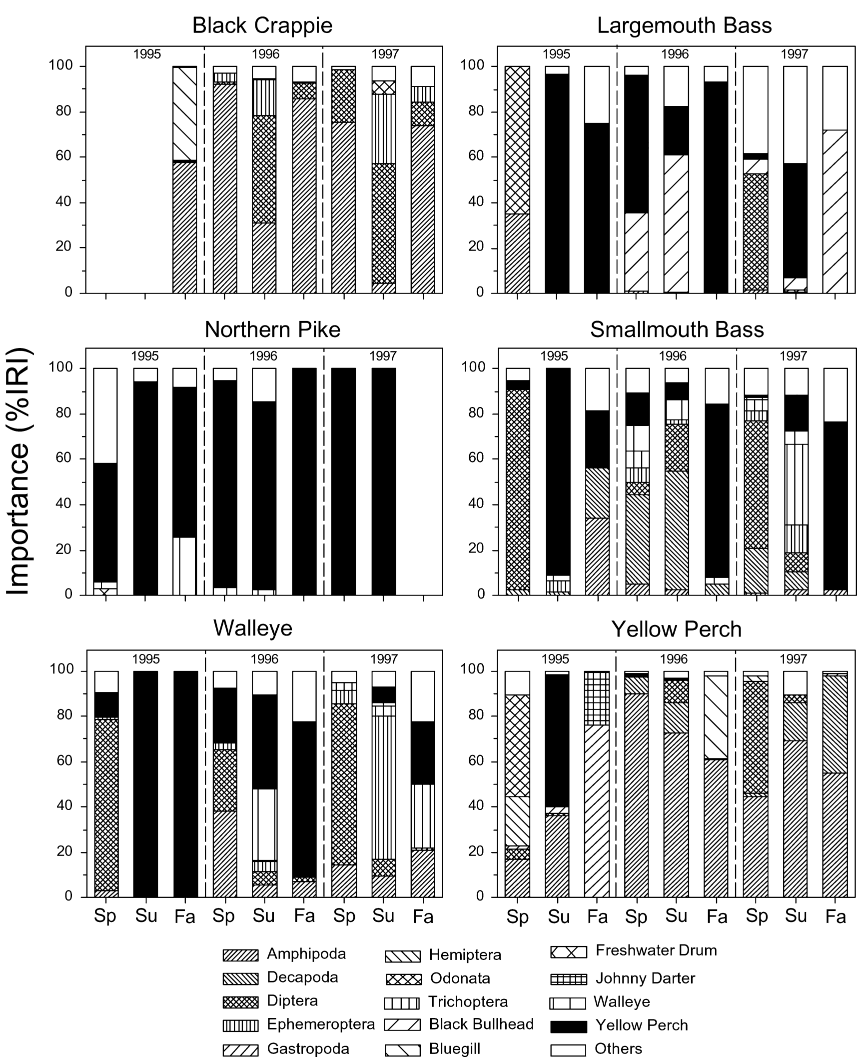


*Fig. 1.* Importance of major prey taxa in the diets of small black crappie, largemouth bass, northern pike, smallmouth bass, walleye, and yellow perch in Spirit Lake, Iowa, USA, 1995–1997. Seasons are indicated as follows: Sp = spring, Su = summer, and Fa = fall. Years are separated by dashed vertical lines. Key to prey taxa is at the bottom of the figure.

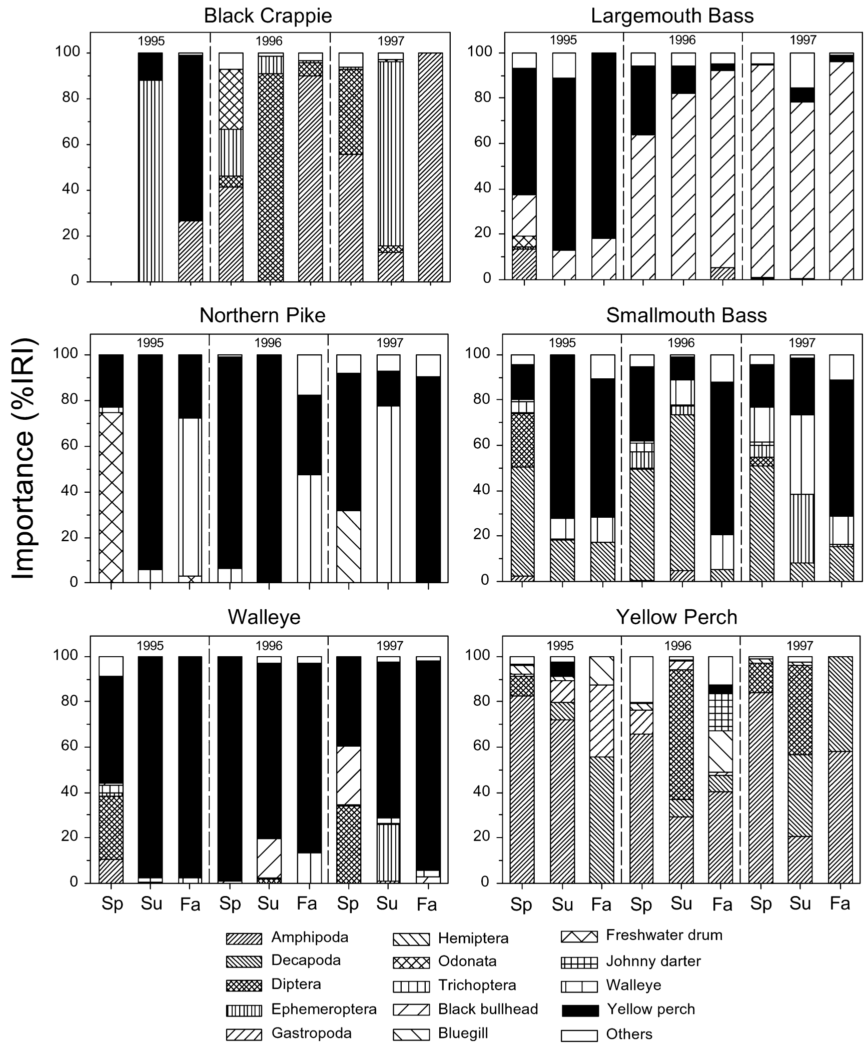


*Fig. 2.* Importance of major prey taxa in the diets of large black crappie, largemouth bass, northern pike, smallmouth bass, walleye, and yellow perch in Spirit Lake, Iowa, USA, 1995–1997. Seasons are indicated as follows: Sp = spring, Su = summer, and Fa = fall. Years are separated by dashed vertical lines. Key to prey taxa is at the bottom of the figure.

Yellow perch and black crappie were the least piscivorous among the six species. Yellow perch diets were dominated by amphipods, dipterans, decapods, and gastropods, averaging roughly 50, 13, 11, and 8% in importance over the study, respectively (Table 2). Amphipods were more important in spring and summer than in fall (Figs 1 and 2). Bluegill, yellow perch, and johnny darter *Etheostomanigrum* (Rafinesque) were occasionally important in the diets of both small and large yellow perch; however, no fish species were important in yellow perch diets in 1997 (Figs 1 and 2).

Black crappie diets were dominated by amphipods, dipterans, and ephemeropterans, averaging roughly 50, 19 and 17% in importance over the study, respectively (Table 2). Bluegill were prominent in small black crappie diets in fall of 1995 (Fig. 1), while in large black crappie diets yellow perch were present in summer and dominant in fall of 1995 (Fig. 2). Both size classes of black crappie showed a decline in importance of fish in their diets after 1995.

## Diet similarities

Figure 3 presents a single ordination, but the comparison units are plotted in three separate panels by year to better display patterns. The stress value of the ordination was 0.18, which indicates a good representation of diet similarities among units in three-dimensional space (Clarke & Warwick 1994).

Walleye and northern pike diets tended to group together in the ordination, typically occurring at low values of Dimension 1, intermediate values of Dimension 2, and intermediate to high values of Dimension 3 (Fig. 3). Diets of both size classes of walleye and northern pike tended to occur together in the ordination space. This separation from the other species was largely due to the predominance of yellow perch and lack of amphipods in the diets. Largemouth bass diets tended to occur at intermediate values of Dimension 1, low values of Dimension 2, and intermediate values of Dimension 3. The separation of

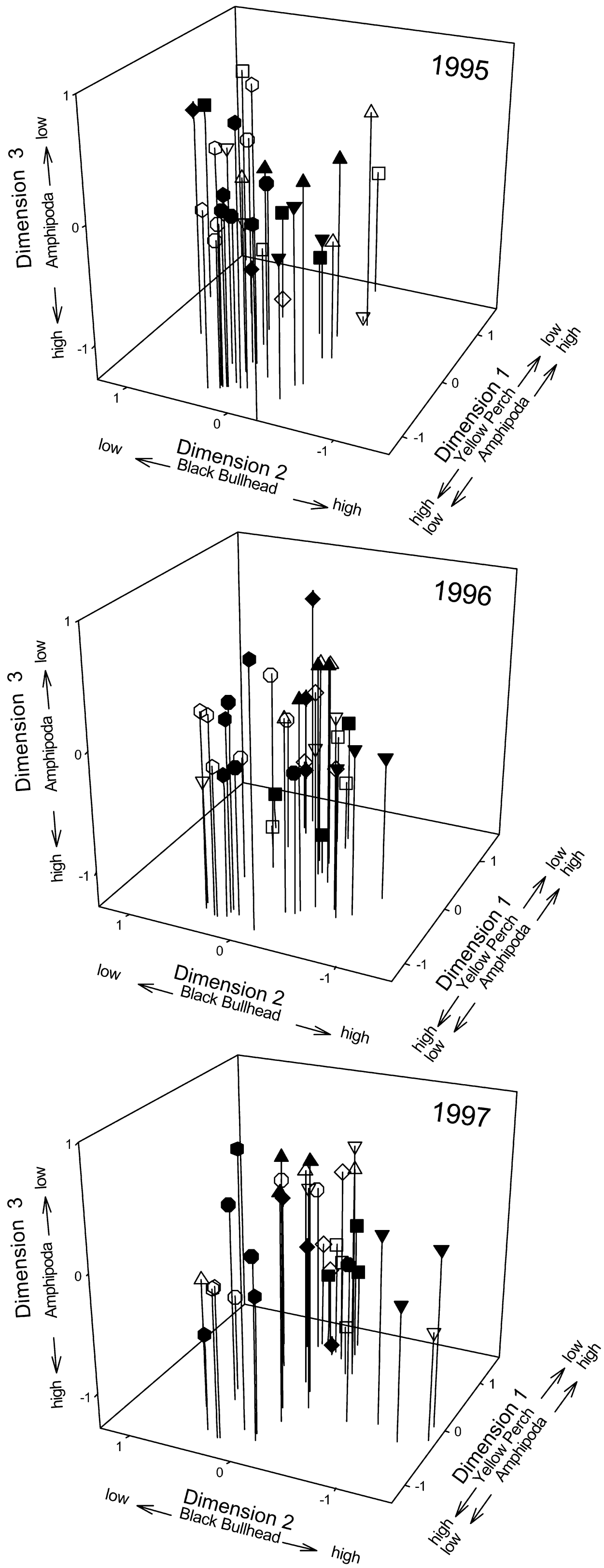


*Fig. 3.* MDS ordination of diet similarities among small and large size classes of piscivorous fish species in Spirit Lake, Iowa, USA, 1995–1997. Ordination was based on a matrix of pair-wise Bray–Curtis similarity coefficients constructed from transformed ($\log_{10}[x+1]$) %IRI values of all prey taxa for each comparison unit. A single ordination was performed, but diets

largemouth bass from the other species, most evident along Dimension 2, was primarily due to the greater importance of black bullhead in largemouth bass diets than any other species. Smallmouth bass diets were more scattered throughout the ordination space than other species, occurring throughout the range of Dimension 1 values, at mostly intermediate values of Dimension 2, and at intermediate to high values of Dimension 3. The wide variation of smallmouth bass diets along Dimension 3 was primarily due to the large variation in importance of yellow perch in different sampling periods. Yellow perch and black crappie diets tended to group together, although there were several exceptions to this pattern. Yellow perch and black crappie diets were usually found at intermediate to high values of Dimension 1, intermediate values of Dimension 2, and intermediate to low values of Dimension 3. This separation from the other species was primarily due to the importance of amphipods and scarcity of yellow perch in the diets.

These patterns in the diet similarities within the piscivore community were supported by our ANOSIM results. The overall test of differences among all piscivorous species was significant (Global $R < 0.001$), and pair-wise tests indicated significantly different diets between all species pairs except walleye–northern pike and yellow perch–black crappie. The overall test of diet differences between size classes was not significant (Global $R = 0.083\%$).

Although patterns of species differences are evident in Fig. 3, there is also ample evidence of within-species variability and among-species overlap in diets. Numerous examples can be found in Fig. 3 where diets from different species were more similar than those of the same species from a different size class, season or year. For example, the diet of small walleye during one season (spring) in 1997 was separated considerably from other walleye diets. This reflected a dramatic difference from diets of both small and large walleye in all other sampling periods (Figs 1 and 2), and a greater similarity to diets of yellow perch and black crappie.

*Fig. 3.* continued
of comparison units were plotted separately by year to reduce clutter. Species listed along ordination axes were significantly ($P < 0.05$) correlated with dimension scores, accounted for at least 50% of the variation ($r \geq 0.7$), and are included to facilitate interpretation. Small size classes are indicated by open symbols; large size classes are indicated by filled symbols. Piscivorous species are indicated by symbol type as follows: walleye (circles), yellow perch (squares), smallmouth bass (triangles up), largemouth bass (triangles down), black crappie (diamonds), northern pike (hexagons).

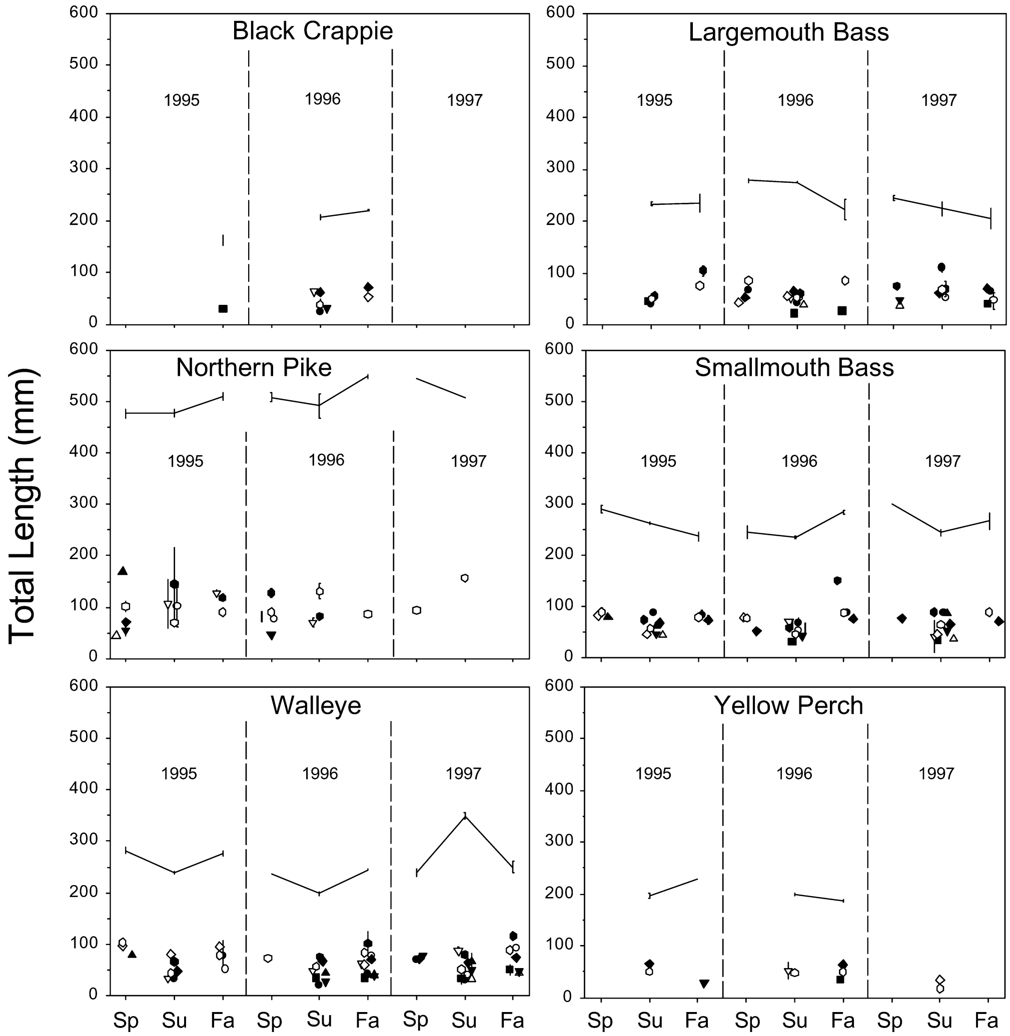


*Fig. 4.* Relative size of major prey fish species in the diets of small black crappie, largemouth bass, northern pike, smallmouth bass, walleye, and yellow perch in Spirit Lake, Iowa, USA, 1995–1997. Seasons are indicated as follows: Sp = spring, Su = summer, and Fa = fall. Years are separated by dashed vertical lines. Mean (SE) predator size is indicated by solid lines. Mean (±SE) prey size is indicated by symbols as follows: black bullhead (filled circle), black crappie (open circle), bluegill (filled square), bigmouth buffalo (open square), freshwater drum (filled triangle up), Iowa darter (open triangle up), johnny darter (filled triangle down), largemouth bass (open triangle down), logperch (filled diamond), spottail shiner (open diamond), walleye (filled hexagon), yellow perch (open hexagon).

### Length of prey fish in diets

Mean lengths of prey fish species in the diets of the six piscivorous species ranged from 10 to 290 mm, averaging 73 mm (Figs 4 and 5). Mean lengths of prey fish typically were 20–30% of the mean lengths of their predators, and very few were greater than 40%. Within predator species, mean prey fish lengths were generally greater in the large size class, although the relative lengths were often less. Larger predator species such as northern pike tended to eat larger prey fish than smaller predator species such as black crappie and yellow perch. No consistent differences in size among prey species were evident.

## Discussion

Our study is the first to document the diet dynamics of six co-occurring adult piscivorous fish species in a natural lake, experiencing the same food resources over three consecutive years. It provides insight into similarities and differences in how these species respond to common food resources. Diets varied considerably among species, and less so between size classes within species. In general, largemouth bass, northern pike, and walleye concentrated primarily on fish prey whereas black crappie and yellow perch concentrated primarily on invertebrate prey. Smallmouth bass diets were somewhat intermediate,

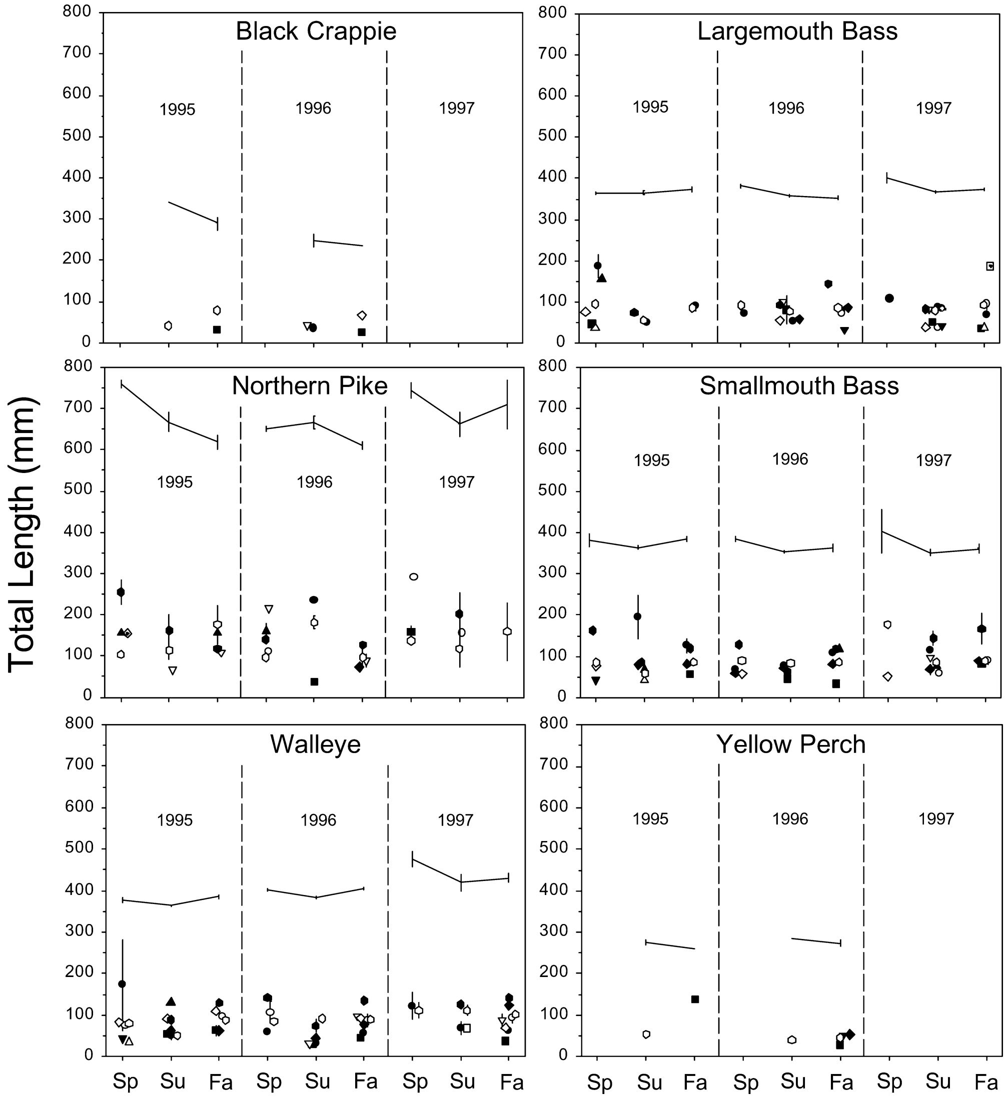


*Fig. 5.* Relative size of major prey fish species in the diets of large black crappie, largemouth bass, northern pike, smallmouth bass, walleye, and yellow perch in Spirit Lake, Iowa, USA, 1995–1997. Seasons are indicated as follows: Sp = spring, Su = summer, and Fa = fall. Years are separated by dashed vertical lines. Mean (SE) predator size is indicated by solid lines. Mean (±SE) prey size is indicated by symbols as follows: black bullhead (filled circle), black crappie (open circle), bluegill (filled square), bigmouth buffalo (open square), freshwater drum (filled triangle up), Iowa darter (open triangle up), Johnny darter (filled triangle down), largemouth bass (open triangle down), logperch (filled diamond), spottail shiner (open diamond), walleye (filled hexagon), yellow perch (open hexagon), white bass (open diamond with x-hair), common carp (open square with x-hair), golden shiner (filled circle with x-hair).

typically containing significant percentages of both fish and invertebrates. Keast (1985) reported diet differences among largemouth bass, northern pike, black crappie, and yellow perch that were similar to our findings.

Pelham et al. (2001) quantified diets of age 0 and age 1 black crappie, largemouth bass, smallmouth bass, walleye and yellow perch in Spirit Lake in 1997–1998. Largemouth bass, smallmouth bass and walleye became piscivorous at age 0, black crappie became piscivorous at age 1, but neither age 0 nor age 1 yellow perch were piscivorous. Our data suggest that differences in the onset and extent of piscivory demonstrated in juveniles of these species persist in adults.

Northern pike and walleye differed from other piscivores in Spirit Lake because of the importance of yellow perch in their diets. Northern pike in Spirit Lake ate yellow perch almost exclusively. Northern pike diets were dominated by yellow perch in some previous studies (e.g., Chapman et al. 1989), but also by other prey fish species such as walleye (Sammons et al. 1994), gizzard shad *Dorosoma cepedianum* (Lesueur) (Wahl & Stein 1993), common carp *Cyprinus carpio* (Linnaeus), and black crappie (Sammons et al. 1994). The identification of yellow perch as the most important prey fish for walleye in our study is consistent with many previous studies (Kelso 1973; Forney 1977; Nelson & Walburg 1977; Nielsen 1980;

Lyons & Magnuson 1987; Ritchie & Colby 1988). Age 0 yellow perch were prominent in the diet of age 1 walleye in Spirit Lake, but absent from the diet of age 0 walleye because they were too large to be eaten (Pelham et al. 2001).

In Spirit Lake, black crappie and yellow perch exhibited low levels of piscivory, concentrating primarily on amphipods. Black crappie diets from previous studies vary significantly. Keast (1985) reported that black crappie became piscivorous at much later ages than largemouth bass and northern pike in Lake Opinicon, Canada. In contrast, in southern USA lakes and reservoirs black crappie may prey significantly on gizzard shad (Reid 1949) and threadfin shad *Dorosoma petenense* (Günther) (Maceina et al. 1991; McInerny & Degan 1991) at earlier ages. Yellow perch typically consume more invertebrates than fish (Hubert & Sandheinrich 1983; Parrish & Margraf 1994), and their degree of piscivory appears to be influenced more by relative invertebrate availability than by prey fish availability (Knight et al. 1984; Hanson & Leggett 1986; Hayward & Margraf 1987; Hayes et al. 1992), suggesting that yellow perch may be more opportunistic than other piscivores. Although our yellow perch diet results are in broad agreement with previous studies, they differ in ranking crayfish as important prey.

The predominant prey fish species in the diets of largemouth bass vary considerably among systems. The major prey has been variously reported to be bluegill (Cochran & Adelman 1982), gizzard shad (Storck 1986), inland silverside *Menidia beryllina* (Cope) (Matthews et al. 1992), walleye (Santucci & Wahl 1993), and yellow perch (Clady 1974; Guy & Willis 1991). Our study adds black bullhead to this list, which distinguished largemouth bass from other species in Spirit Lake. In addition to yellow perch, Pelham et al. (2001) reported significant percentages of johnny darters and bluegill in age 1 largemouth bass diets in Spirit Lake.

Smallmouth bass diets included a high percentage of crayfish, and a fairly equal split between percentages of invertebrates and fish. Previous studies of adult smallmouth bass diets reported similar results (Clady 1974; Johnson & Hale 1977; Scott & Angermeier 1998), as did Pelham et al. (2001) for age 1 smallmouth bass in Spirit Lake.

Diets included greater percentages of fish prey and larger fish prey as piscivores grew, which is consistent with previous studies (Reid 1949; Keast 1977; Knight et al. 1984; Storck 1986; Sammons et al. 1994; Scott & Angermeier 1998). Juvenile black crappie, largemouth bass, smallmouth bass and walleye demonstrated similar ontogenetic diet changes in Spirit Lake (Pelham et al. 2001).

Seasonal changes in the diets of most species were detected in this study. For example, importance of amphipods in the diet of small yellow perch decreased steadily in 1996. Another example was the steady increase in importance of yellow perch in the diet of large walleye in 1997. An exception to this general pattern of seasonal changes in diet was small northern pike, which fed on yellow perch almost exclusively throughout the study. Invertebrates and small prey fish were more important early in the year in most species, whereas relatively large prey fish were more important later in the year.

Yearly variation in the diets of piscivorous species was also noted. Small largemouth bass shifted from preying primarily on yellow perch to other taxa, while large largemouth bass shifted from a diet dominated by yellow perch to a diet consisting almost exclusively of black bullhead between 1995 and 1997. Small walleye consumed a higher percentage of invertebrates in 1997 than in previous years. Large black crappie and small yellow perch consumed low percentages of fish in 1997, a decrease from 1995 and 1996. Large smallmouth bass consumed more large prey fish such as walleye in 1997 than in previous years. A trend evident throughout much of the piscivore community was a gradual decrease in importance of yellow perch from 1995 to 1997, although they were still important to small northern pike and large walleye in 1997. Other than the general decrease in importance of yellow perch, these yearly changes were asynchronous among species and even among size classes within species, despite occurring simultaneously in a common environment. Clearly, piscivores in Spirit Lake responded differently over time to a common suite of prey resources.

Although our results for individual species were generally in qualitative agreement with previous studies, we found that temporal diet changes in the two size classes of the six species we examined were complex and often asynchronous. This serves as a reminder of the potential discrepancy between apparent prey availability, as measured by sampling prey abundance, and realized availability to predators as measured by importance in their diets. Had this relationship been simple and direct, we would have expected much greater among-species diet similarity through time. Piscivorous species exhibit different foraging behaviors, habitat use, trophic morphology, relative predator–prey body size and other factors that can result in strikingly different diets obtained from a common suite of available prey resources.

These differences underscore the potentially complex impact that the collective consumption of a diverse piscivorous community, such as the one in Spirit Lake, can exert on available prey resources.

## Resumen

1. Las dietas de adultos de seis especies piscívoras, *Pomoxis nigromaculatus*, *Micropterus salmoides*, *M. Dolomieui*, *Esox lucius*, *Stizostedium vitreum* y *Perca flavescens*, fueron cuantificados en el Lago Spirit (Iowa, USA) desde Mayo a Octubre en los años 1995 a 1997.
2. Cuarenta y taxones presas fueron encontrados en las dietas de estas 6 especies incluyendo 19 especies de peces. Los taxones presa mas importantes de fueron *P. flavescens*, amfipodos y dipteros. Mientra que las dietas de *E. Lucius* y *S. Vitreum* estuvieron dominadas *por P. flavescens*, la dieta de *M. salmonides* incluyó grandes porcentajes de *P. flavescens* y *Ameiurus melas* y la de *M. Dolomieui*, grandes porcentajes de *P. flavescens* y cangrejos. A su vez, las dietas de *P. nigromaculatus* y *P. flavescens* estuvieron dominadas por invertebrados, primariamente anfípodos y dípteros.
3. Detectamos diferencias pronunciadas en las dietas entre las especies, entre clases de tamaños de cada especie y a lo largo del tiempo. La mayor parte de los taxones presas dominantes en las dietas de estos piscívoros concordaron con estudios previos pero unos pocos se desviaron significativamente de lo esperado. Muchos de los cambios temporales en las dietas no fueron sincrónicos entre las especies y las clases de tamaños sugiriendo respuestas diferentes a cambios temporales en los recursos presas.

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